A SYNOPSIS OF THE GENUS *ECHINOPEPON* (CUCURBITACEAE: SICYEAE), INCLUDING THREE NEW TAXA[1]

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ABSTRACT

Following a palynological and general morphological survey, the genus *Echinopepon* (Cucurbitaceae) has been divided into three species groups on the basis of stamen and pollen morphology. Three new species of *Echinopepon* are described and illustrated: *E. tultitlanapaensis* A. K. Monro & Staff., *E. belizensis* A. K. Monro & Staff., and *E. microparviculatus* A. K. Monro & Staff.; three new combinations are proposed: *E. arachoides* (Dieterle) A. K. Monro & Staff., *E. gemellus* (DC.) A. K. Monro & Staff., and *E. glutinosus* (Cogn.) A. K. Monro & Staff.; and *E. floribundus* (Cogn.) Rose is reduced to synonymy of *E. pubescens* (Benth.) Rose. A nomenclatural review is presented, and the 18 species of the genus *Echinopepon* are listed, together with the specimens examined.

Echinopepon (Cucurbitaceae) is a genus of 18 New World taxa whose center of diversity is the Pacific coast of Mexico at middle to high elevations (above 1000 m) in the Sierra Madre Occidental and the Sierra Madre del Sur. While preparing accounts of *Echinopepon* for *Flora Mesoamericana*, it became clear that this genus was in great need of nomenclatural and systematic revision. Previous palynological work on the genus (Stafford & Sutton, 1994) and systematic treatments of the family (Jeffrey, 1964; Rangaswami Ayyangar, 1976) indicated that a synoptic revision of the genus based on macromorphological and palynological observations would be appropriate.

Echinopepon is one of four genera to have been separated from the genus *Sicyos* L. as originally proposed in *Hortus Cliffortianus* in 1737 (Stocking, 1955). In 1840, Torrey and Gray formed a separate genus of the New World taxa in the Linnaean *Sicyos*, which they named *Echinocystis*. Over the next decade *Echinocystis* was divided into three sections, *Echinocystis* ("*Euechinocystis*"), *Echinopepon*, and *Marah* (Cogniaux, 1877; Cogniaux, 1881), which were later recognized at generic rank by Watson (1887, in which he referred to *Marah* Kellogg under the synonym: *Megarrhiza* Torr.).

Despite further papers on the nomenclature and taxonomic status of *Echinopepon* (Watson, 1889; Rose, 1897; Stocking, 1955), the genus has not been comprehensively reviewed since 1881, when Cogniaux treated it as a section of *Echinocystis*.

GENERAL MORPHOLOGY

The principal characters used to classify subfamilies, tribes, and subtribes in the family Cucurbitaceae relate to the pistil, stamens, tendrils, and pollen (Cogniaux, 1877; Jeffrey, 1990). Within the tribe Sicyeae, anther arrangement, the disposition of the ovules within the ovary, fruit and seed morphology, and the branching of tendrils have been used to define the genera (Jeffrey, 1990). Naudin (1866) defined *Echinopepon* as monoecious, with 5–6-merous flowers, having three fused stamens (one unilocular and two bilocular), a unilocular ovary bearing 8–10 ovules, a 2-chambered, coriaceous, cylindrical fruit possessing a dehiscent, apical operculum, and seeds that are ovoid-compressed and corrugate.

Within the genus *Echinopepon* itself, inflorescence disposition, flower size, the disposition of the anther thecae, the relative length of the corolla lobes to the hypanthium, and fruit size, shape, and spine-length have all been used to distinguish taxa (Naudin, 1866; Cogniaux, 1877; Rose, 1897; Watson, 1889).

[1] We thank Helen Greenop for the botanical drawings, Lourdes Rico (K) for help with Mexican localities, Carol Furness (K) for pollen samples of *Echinopepon jaliscanus*, Philipe Morat for a warm reception at P, Charlie Jarvis (BM) for help with nomenclature, Norman Robson (BM) for help with the Latin diagnoses, Bob Press (BM), Sandra Knapp (BM), and Mary Gibby (BM) for help with the manuscript, and the following herbaria for the loan of reference material: B, BR, F, GH, GOET, MA, MO, NY, P, and US.

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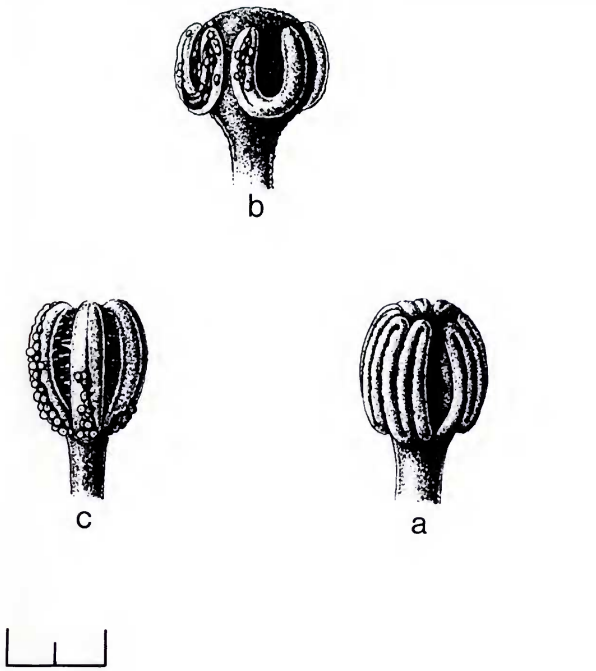

Figure 1. —a. Anther of the *Echinopepon racemosus* species group.—b. Anther of the *E. torquatus* species group.—c. Anther of the *E. paniculatus* species group. Scale bar = 1 mm.

Pollen Morphology

Pollen characters in the family Cucurbitaceae show a high degree of diversity and have long been perceived as indicators of relationships at all taxonomic levels. In an overview of pollen morphology in the Cucurbitaceae, Jeffrey (1964) found that his earlier conventional classifications of the family (Jeffrey, 1961, 1963) corresponded to a high degree with the natural order of taxa as indicated by pollen morphology, "much more so than any previous classification scheme." Rangaswami Ayyangar (1976)

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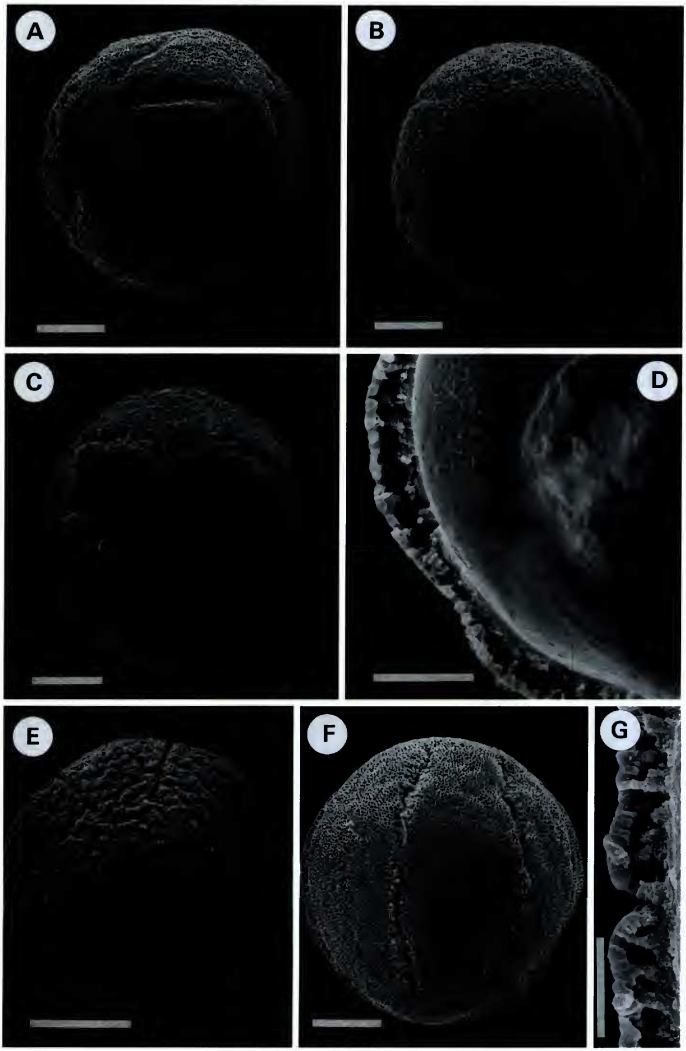
Figure 2. Polypantocolpate to irregularly syncolporate pollen type (SEM micrographs).—A. *Echinopepon racemosus* (scale bar = 25 μm).—B. *E. tultitlanapaensis* (scale bar = 25 μm).—C. *E. jaliscanus.* Note branching colpi (scale bar = 25 μm).—D. *E. racemosus.* Section showing exine stratification (scale bar = 8 μm). 6–8-zonocolpate pollen type.—E. *E. coulteri.* Polar view (scale bar = 20 μm).—F. *E. coulteri.* Equatorial view (scale bar = 25 μm).—G. *E. coulteri.* Section showing exine structure (scale bar = 5 μm).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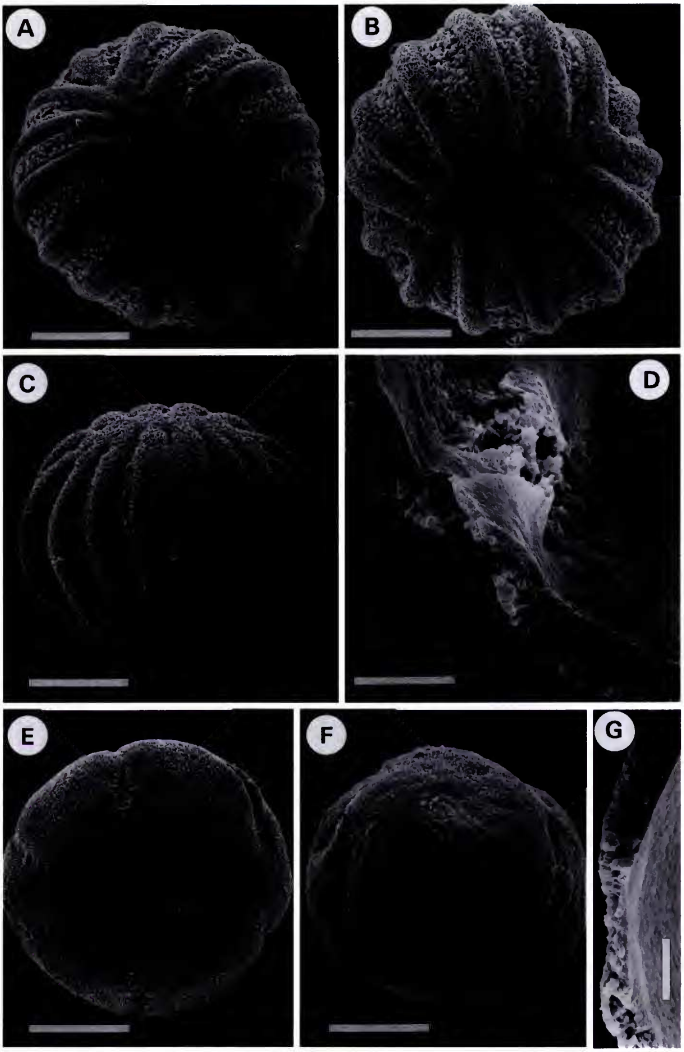
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also found that dividing the family into seven tribes on a palynological basis agreed with his own previous classification (Rangaswami Ayyangar, 1967) based on karyological characters (although it was not highly congruent with Jeffrey's classification).

Except in the case of *Echinopepon*, pollen morphological divisions within the subtribe Cyclantherinae otherwise correspond almost perfectly with present generic boundaries (Stafford & Sutton, 1994). In a general account of pollen morphology in the Cyclantherinae, Stafford and Sutton (1994) grouped the pollen of a selection of species representing each of the genera into seven main types, within which taxa can be further identified to generic and, in some cases, to specific level.

Pollen of the genus *Echinopepon* is particularly variable. Stafford and Sutton (1994) indicated that three or more conspicuous pollen types could be identified within *Echinopepon*, which conform to the groupings of Jeffrey (1980).

In the light of these distinct infrageneric groupings, an analysis of pollen characters in *Echinopepon* and related genera has been undertaken which extends preliminary work conducted by Stafford and Sutton (1994).

Materials and Methods

All the taxa in the genus *Echinopepon* and representative taxa from the related genera *Echinocystis*, *Marah*, *Brandegea*, and *Vaseyanthus* were studied. For *Echinopepon* the extant type material was examined, although it was not always possible to include these in the palynological review. In addition, all of the specimens at K, BM, and P were seen, as were selected specimens from BR, F, GH, GOET, MA, MO, NY, and US. Specimens were examined by eye and at a magnification of ×64 to ×400 under a Leitz Wild M3C microscope.

The following characters were found to be of particular value: indument of the leaf, petiole, stem, and fruit; staminate and pistillate inflorescence type; staminate and pistillate perianth morphology; fruit spine length; seed ornamentation; and pollen morphology.

Pollen samples from each of the specimens studied were prepared by acetolysis (Erdtman, 1969). Due to the thin nature of the exine, acetolysis time was restricted in some cases to two or three minutes to minimize pollen collapse. A small portion of the acetolyzed residue was mounted on aluminum stubs for scanning electron microscopy (SEM), and the remaining material was used to prepare microscope slides for light microscopy. Observations were made using a Zeiss Axioplan light microscope and a Hitachi S800 field emission scanning electron microscope, using secondary electron detection and an accelerating voltage of 8 kV. Material for observation in the SEM was first sputter coated with gold palladium for one and a half minutes at 20 mA. The following parameters were measured: polar axis (P), equatorial axis (E), grain symmetry, number and character of colpi, exine thickness at center of mesocolpium, and ornamentation characteristics. Measurements were made from light microscope preparations in glycerine jelly, and are based on an examination of ten pollen grains from each specimen.

Results

Anther morphology falls into three groups: obovoid anthers with the thecae appearing 2–3-sigmoid (Fig. 1a); subglobose anthers with the thecae appearing "horse-shoe"-shaped (Fig. 1b); and ovoid anthers with the thecae appearing "banana"-shaped (Fig. 1c).

The pollen of the genus *Echinopepon* is remarkably variable and may be grouped into four distinct pollen types:

Pollen type 1 (Fig. 2A–D). Grains polypantocolpate to irregularly syncolporate; colpi short, sometimes branched and fused, dividing the exine into angular plates; endoaperture a weak, circular thinning of the nexine, distinguishable in the scanning electron microscope but indistinct in light microscopy; exine thin and of three layers: nexine thin with covering of coarse granules, sexine 1 of sparsely distributed columellae, sexine 2 a relatively thin perforated tectum; ornamentation punctitegillate. Size range: longest axis 85–164 μm. Species: *Echinopepon racemosus, E. pringlei, E. tultitlanapaensis, E. jaliscanus.*

Pollen type 2 (Fig. 3A–D). Grains 10–16-zonocolpate, radially asymmetrical with sunken colpi; colpus long, broad and conspicuous, usually with

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Figure 3. Polyzonocolpate pollen type (SEM micrographs).—A. *Echinopepon torquatus.* Polar view (scale bar = 25 μm).—B. *E. arachoides.* Polar view (scale bar = 20 μm).—C. *E. cirrhopedunculatus.* Equatorial view (scale bar = 25 μm).—D. *E. torquatus.* Section of colpus showing exine stratification (scale bar = 5 μm). 6–9-zonocolpate to zonocolporate pollen type.—E. *E. micropaniculatus.* Polar view (scale bar = 20 μm).—F. *E. belizensis.* Equatorial view (scale bar = 20 μm).—G. *E. pubescens.* Section showing exine stratification (scale bar = 12 μm).

elaborate, distinctly granular margins and a margo (see Fig. 3A–C); exine of three layers, thickest at center of mesocolpium with corresponding thinning of nexine and sexine toward colpi: nexine thin, without covering of granules, sexine 1 of densely spaced columellae, sexine 2 a perforated tectum; ornamentation punctitegillate. Size range: P60–148 μm, E60–135 μm. Species: *Echinopepon torquatus, E. milleflorus, E. gemellus, E. cirrhopedunculatus, E. arachoides, E. minimus.* This pollen type also embraces *Apatzingania* Dieterle (herein synonymized with *Echinopepon*).

Pollen type 3 (Fig. 2E–G). Grains 6–8-zonocolpate, radially symmetrical, colpi not or only slightly sunken; colpus long and narrow without any marginal differentiation of the exine; exine thin and of three layers: nexine very thin, with covering of fine granules, sexine 1 of broadly spaced columellae, sexine 2 a relatively thin, perforated tectum; ornamentation punctitegillate to weakly verrucate. Size range: P85–135 μm, E95–110 μm. Species: *Echinopepon coulteri.*

Pollen type 4 (Fig. 3E–G). Grains 6–9-zonocolpate to -zonocolporate; colpus long, broad, and conspicuous, with granular surface, sunken; endoaperture when present a poorly defined circular pore, arranged alternately above and below the equator and rarely on the equatorial plane itself, sometimes characterized by a raised annulus; exine of three layers: nexine thin, without covering of granules, sexine 1 of densely spaced columellae, sexine 2 a perforated tectum; ornamentation punctitegillate. Size range: P74–104 μm, E70–94 μm. Species: *Echinopepon paniculatus, E. glutinosus, E. wrightii, E. pubescens, E. longispinus, E. belizensis, E. micropaniculatus.*

Discussion

On the basis of the above characters we suggest that the genus *Echinopepon* be divided into three clearly defined species groups, as outlined below. We feel that one of these, the *racemosus* group, may well represent a distinct genus. In view of the fact that this tribe (Sicyae) and subtribe (Cyclantherinae) are among the least well known in the Cucurbitaceae (Jeffrey, 1964), the related genera in this tribe require further investigation before such a taxonomic decision can be made.

The monospecific genus *Apatzingania* Dieterle shows many similarities to *Echinopepon* in both palynology and macromorphology (Dieterle, 1974). *Apatzingania* is distinguished from *Echinopepon* by the presence of a unilocular, single-seeded, indehiscent fruit. We interpret these characters as adaptational consequences of geocarpy. The pollen most closely resembles that of *E. cirrhopedunculatus*, a taxon whose fruit, although not geocarpous, is also borne on an exceptionally long peduncle and whose seeds are very similar in their ornamentation. Although the habit of geocarpy is extremely rare in the Cucurbitaceae (the only other species is the South African *Cucumis humifructus* Stent), geocarpy by itself may not be sufficient reason for distinguishing *Apatzingania* as a separate genus. In consideration of this and the morphological similarities outlined above, we include *Apatzingania arachoidea* Dieterle in the genus *Echinopepon.*

Conspectus of the genus *Echinopepon*

I. *E. racemosus* species group

Flowers campanulate; anther obovoid; thecae appearing tubular prior to dehiscence after which ribbon-like, folded into 2- and 3-sigmoid curves (Fig. 1a); pollen polypantocolpate to irregularly syncolporate (Fig. 2A–D).

1. *Echinopepon racemosus* (Steud.) C. Jeffrey
2. *E. pringlei* Rose
3. *E. tultitlanapaensis* A. K. Monro & Staff.
4. *E. jaliscanus* Rose

II. *E. torquatus* species group

Flowers campanulate to infundibuliform; anther subglobose; thecae "horse-shoe"-shaped, appearing tubular prior to dehiscence after which ribbon-like (Fig. 1b); pollen 10–16-zonocolpate and radially asymmetrical, the colpus margins distinctly differentiated and granular (Fig. 3A–D); or 7–9 symmetrically zonocolpate, the colpus margins undifferentiated (*E. coulteri,* Fig. 3E–G).

5. *Echinopepon torquatus* (DC.) Rose
6. *E. milleflorus* Naudin
7. *E. gemellus* (DC.) A. K. Monro & Staff.
8. *E. coulteri* (A. Gray) Rose
9. *E. cirrhopedunculatus* Rose
10. *E. arachoides* (Dieterle) A. K. Monro & Staff.
11. *E. minimus* (Kellogg) S. Watson

III. *E. paniculatus* species group

Flowers campanulate to infundibuliform; anther subglobose; thecae "banana"-shaped, appearing tubular prior to dehiscence after which ribbon-like (Fig. 1c); pollen 6–8-zonocolporate and radially asymmetrical with indistinct endoapertures, the colpus margins undifferentiated and not granular (Fig. 3E–G).

12. *Echinopepon paniculatus* (Cogn.) Dieterle
13. *E. glutinosus* (Cogn.) A. K. Monro & Staff.
14. *E. wrightii* (A. Gray) S. Watson
15. *Echinopepon pubescens* (Benth.) Rose
16. *E. longispinus* (Cogn.) Rose
17. *E. belizensis* A. K. Monro & Staff.
18. *E. micropaniculatus* A. K. Monro & Staff.

Taxonomic Synopsis

This synopsis presents a key to all of the species of *Echinopepon* discussed above. Full descriptions are only given for previously undescribed taxa. However, full nomenclature, including synonymy and literature citations, is given for each taxon together with a list of all specimens examined.

Key to the Species of *Echinopepon*

All inflorescence and floral characters refer to those of staminate flowers only.

1a. Peduncle of mature fruit thread-like, 60–80 mm in length at maturity.
  2a. Fruit geocarpous, lacking an apical operculum ..... *E. arachoides*
  2b. Fruit not geocarpous, with an apical operculum ..... *E. cirrhopedunculatus*
1b. Peduncle of mature fruit not thread-like, more robust, 3–45 mm in length at maturity.
  3a. Peduncle of mature fruit glabrous.
    4a. Leaves weakly lobed to entire; inflorescences with fewer than 25 flowers ..... *E. milleflorus*
    4b. Leaves profoundly lobed; inflorescences with more than 25 flowers ..... *E. torquatus*
  3b. Peduncle of mature fruit pubescent, occasionally only sparsely so.
    5a. Hypanthium glabrous; anther thecae never folded into 2- to 3-sigmoid curves.
      6a. Corolla lobes 6–10 mm in length ..... *E. paniculatus*
      6b. Corolla lobes 2–4.5 mm in length.
        7a. Petiole glabrous, although occasionally with small, white plate-like structures; anther thecae "horse-shoe"-shaped.
          8a. Unbranched portion of tendrils 4–10 mm long; pedicel 3–5 mm long ..... *E. gemellus*
          8b. Unbranched portion of tendrils 10–65 mm long; pedicel 10–20 mm long ..... *E. minimus*
        7b. Petiole densely pubescent; anther thecae "banana"-shaped.
          9a. Pedicel 3–5 mm long; anthers fused to form an ovoid or obovoid head ..... *E. micropaniculatus*
          9b. Pedicel 8–10 mm long; anthers fused to form a subglobose head ..... *E. wrightii*
    5b. Hypanthium pubescent; anther thecae "horse-shoe"-shaped, "banana"-shaped, or folded into 2- to 3-sigmoid curves.
      10a. Corolla less than 5 mm in length; anther thecae "banana"-shaped.
        11a. Pedicel 4–6 mm long; fused filaments subsessile, less than 0.2 mm long ..... *E. glutinosus*
        11b. Pedicel 8–10 mm long; fused filaments ca. 1 mm long ..... *E. wrightii*
      10b. Corolla 5 mm or more in length; anther thecae folded into 2–3-sigmoid curves or, "horse-shoe"-shaped.
        12a. Inflorescence branched.
          13a. Inflorescences with 12–20 flowers; fruit more than 50 mm in length ..... *E. belizensis*
          13b. Inflorescences with 90–120 flowers; fruit less than 50 mm in length ..... *E. longispinus*
        12b. Inflorescence unbranched.
          14a. Thecae not folded into 2- to 3-sigmoid curves.
            15a. Corolla 5–8 mm long; anther thecae "horse-shoe"-shaped ..... *E. coulteri*
            15b. Corolla 12–18 mm long; anther thecae "banana"-shaped ..... *E. pubescens*
          14b. Thecae folded into 2- to 3-sigmoid curves.
            16a. Corolla divided to less than half its length; peduncle of mature fruit less than 8 mm in length.
              17a. Inflorescences 80–340 mm long; corolla (12)16–22 mm diam.; anthers fused to form an obovoid head 3–3.5 mm long ..... *E. jaliscanus*
              17b. Inflorescences 45–95 mm long; corolla 7–10 mm diam.; anthers fused to form an ovoid or obovoid head 2 mm long ..... *E. tultitlanapaensis*
            16b. Corolla divided to more than half its length; peduncle of mature fruit greater than 10 mm in length.
              18a. Calyx lobes ca. 1 mm long ..... *E. pringlei*
              18b. Calyx lobes 2–4.5(–9) mm long ..... *E. racemosus*

1. Echinopepon racemosus (Steud.) C. Jeffrey, Kew Bull. 33: 357. 1979. *Momordica muricata* Vell., Fl. flumin. 10: t. 94. 1831, non Willd. (1805). *Momordica racemosa* Steud., Nomencl. bot. Ed. 2, 2: 155. 1841. *Echinocystis racemosa* (Steud.) Mart. Crov., Notul. Syst. (Paris) 9: 56. 1955. TYPE: t. 94 in Vell., Fl. flumin. 10. 1831 (holotype).

Echinopepon horridus Naudin, Ann. Sci. Nat., Bot. sér. 5, 6: 19. 1866. TYPE: material cultivated in Paris from seed sent from Mexico by Bourgeau in 1865–1866 (holotype, P; isotype, GH n.v.).

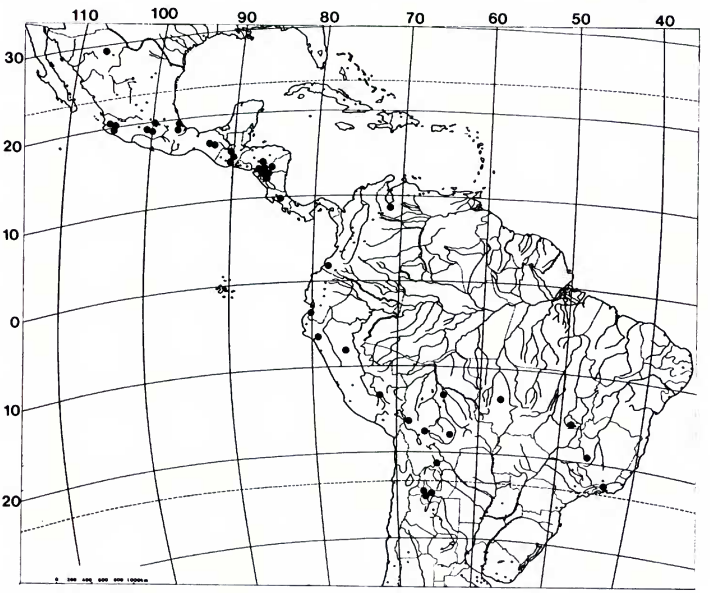

Figure 4. Distribution of *Echinopepon racemosus*.

Echinocystis polycarpa Cogn., Diagn. Cucurb. Nouv. 2: 90. 1877. TYPE: Venezuela. *Ernst 940* (syntype, BM); Venezuela, Colonia Tovar, *Fendler 503* (syntype, K); Colombia. *Triana 3017* (syntype, P).

Echinocystis lanata Cogn., Diagn. Cucurb. Nouv. 2: 92. 1877. TYPE: Mexico. *Galeotti s.n.* (syntype, BR); Mexico. *Liebmann 49* (syntype, C).

Echinocystis araneosa Griseb., Symb. fl. argent. 135. 1890. TYPE: Argentina, *Lorentz & Hieronymus 551* (holotype, BR; isotypes, GOET, K).

Distribution. From northern Mexico (Baja California Sur, Chihuahua) to northern Argentina (Salta Province) at elevations of 300–3500 m (Fig. 4).

Additional specimens examined. MEXICO. **Chiapas:** *Breedlove 13896*[3] (F*, K), *Breedlove & Raven 13157* (K, NY), *Laughlin 2166* (K), *Lira 957* (BM*). **Chihuahua:** *Gentry 2645* (K). **Jalisco:** *Lott 1315* (K), *Botter 573* (K), *Lott 609* (K), *Bullock 1267* (K). **México:** *Hinton 14694* (K), *Hinton 2524* (K), *Hinton 4963* (K), *Hinton 8619* (K). **Oaxaca:** *Carlson 4150* (F). **Veracruz:** *Nee 23573* (K), *Bourgeau 1478* (P), *Bourgeau 3266* (K). GUATEMALA. **Alta Verapaz:** *von Tuerckheim 1099* (K), *Wilson 40897* (F), *Williams 40316* (F), *Williams et al. 40361* (MO, NY, F). **Baja Verapaz:** *Hawkes 1939* (K); Jutiapa, *Steyermark 30378* (F), *Heyde & Lux 4188* (K). HONDURAS. **El Paraíso:** *Hawkes et al. 2055* (F, K), *Molina 23380* (F, MO, NY), *Molina 8688* (F), *Rodríguez 1893* (F). **Francisco Morazán:** *Chorley 374* (BM*), *Escobar 126** (MO), *Lezama 88* (MO), *Molina 24563* (NY*, MO), *Molina 730* (MO). NICARAGUA. **Estelí:** *Moreno 22570* (K), *Moreno 18406* (K), *Moreno 22352* (K), *Stevens & Krukoff 16221* (K, NY). **Jinotega:** *Molina 27288* (F), *Molina 22947* (F, NY), *Stevens 22580* (BM, K), *Williams et al. 24750* (NY), *Williams & Molina 42753* (F*). COSTA RICA. Locality unknown: *Echeverría 877* (F), *Lankester 130* (K), *León 259* (F). **Cartago:** *James 79* (F), *Cooper 5775* (K), *Echeverría 203* (F), *Torres 79* (F).

VENEZUELA. Locality unknown: *André 2809* (K), *Fendler 609* (K). BRAZIL. Locality unknown: *Pohl 1996* (K), *Burchell 6122* (K). **Distrito Federal:** *de Paula & Conçeicao 1537* (K). **Mato Grosso:** *Hatschbach 34110* (K). **Minas Gerais:** *Glaziou 19380* (K). **Rio de Janeiro:** *Glaziou 12739* (K). BOLIVIA. Locality unknown: *Buchtien s.n.* (K), *Lectrae 533* (K). **Cochabamba:** *Eyerdam 25318* (K). **La Paz:** *Fiebrig 2750* (K*), *Solomon 8921* (K). **Santa Cruz:** *Beck 6487* (K). **Tarija:** *Solomon 10073* (K). PERU. Locality unknown: **Cajamarca:** *Sagástegui 12980* (K), *Sagástegui 11419* (K). **Cuzco:** *Stork 10500* (K). **Tumbes:** *Weberbauer 7726* (K). **San Martín:** *Young 241* (K). AR-

[3] An asterisk (*) denotes source of pollen for this study.

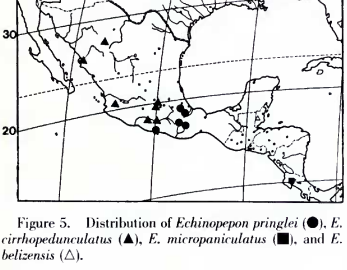

Figure 5. Distribution of *Echinopepon pringlei* (●), *E. cirrhopedunculatus* (▲), *E. micropaniculatus* (■), and *E. belizensis* (△).

GENTINA. Locality unknown: *Lorentz & Hieronymus 552* (K), *Lorentz & Hieronymus 551* (K). **Salta:** *Krapovickas 28245* (K), *Pedersen 12846* (K), *Pedersen 12842* (K).

2. Echinopepon pringlei Rose, Contr. U.S. Natl. Herb. 5: 117. 1897. TYPE: Mexico. Morelos: *Pringle 6183* (holotype, GH; isotypes, BM*, P).

Distribution. Southern Mexico (Veracruz to Oaxaca) at elevations of ca. 1500–2500 m (Fig. 5).

Additional specimens examined. MEXICO. **Oaxaca:** *Galeotti 1880* (K), *Barnes & Lord 474* (K), *Pringle 4958* (BM*). **Veracruz:** *Galeotti 1899* (K).

3. Echinopepon tultitlanapaensis A. K. Monro & Staff., sp. nov. TYPE: Mexico. Puebla: San Luis Tultitlanapa, *Purpus 3548* (holotype, BM*; isotypes, F, GH, MO, NY, US). Figure 6a, b.

E. pringlei Rose affinis, sed corolla profundiore incisa, antheris maioribus, staminorum longiori columna, fructu parvo, bene differt.

Leaves ca. 5.0–6.5 × 4–7 cm, lobate, chartaceous, upper and lower surface strigose to hispid, the trichomes with broad multicellular bases; lobes 3, 5, or 7, the base subsagittate, the margins remotely denticulate, the apex acuminate; petiole ca. 12–27 × 1 mm, densely villous; tendrils bifid, ca. 5–6 cm long before branching. Staminate flowers ca. 9–12, borne in a raceme ca. 4.5–9.5 cm long bearing flowers for ⅓ of its length; pedicel ca. 4–5 × 0.3 mm, pilose to villous; hypanthium ca. 3–4 × 2–3 mm, campanulate, villous; calyx lobes ca. 2 mm long, spiciform to filiform; corolla ca. 7–10 mm long, broadly campanulate, fused for ⅓ of its length, inner surface glabrous, outer surface sparsely pilose to villous, lobes ovate, the apices acute; filaments ca. 2 mm in length, fused; anthers ca. 2 mm in length, fused to form an obovoid head 1.2 mm diam.; unilocular and bilocular thecae 3-sigmoid, glabrous; pollen pantocolporate to syncolporate, colpi 18–24, branched. Pistillate flowers solitary; pedicel ca. 5 × 0.5 mm, villous; hypanthium ca. 2 × 3 mm, broadly campanulate, sparsely puberulous, constricted at base, constriction ca. 4–5 × 0.5 mm, puberulous; calyx lobes ca. 2–3 mm long; corolla ca. 10 × 7 mm, infundibuliform, fused for ⅓ of its length, inner surface glabrous, outer surface sparsely puberulous, lobes ovate, the apices acute; ovary ca. 6–7 mm, ovoid, pilose to villous, spines ca. 3–5 mm; style ca. 2–2.5 mm, glabrous; stigma ca. 1 × 1.5 mm. Fruiting peduncle ca. 4–6 mm, puberulous; fruit ca. 22–37 × 10–12 mm; spines ca. 10–17 mm, pilose; seeds 5 per locule, ca. 5 × 3.5 × 2 mm, obovoid.

Distribution. Known only from the type collection at an elevation of ca. 2000–3000 m (Fig. 7).

This species most closely resembles *Echinopepon pringlei* in that it has a broadly campanulate hypanthium, 2- and 3-sigmoid anther thecae, and pantocolpate pollen. It differs, however, with respect to the perianth and stamens. The perianth of *E. tultitlanapaensis* is larger and the corolla lobes are fused for only ⅓ of their length (compared to ⅔ in *E. pringlei*), causing them to spread to a much greater extent. In addition, the anthers of *E. tultitlanapaensis* are significantly larger, glabrous, and attached to longer filaments. The name is derived from the locality of the type collection, San Luis Tultiltanapa.

4. Echinopepon jaliscanus Rose, Contr. U.S. Natl. Herb. 5: 117. 1897. TYPE: Mexico. Jalisco: *Pringle 4563* (holotype, US n.v.; isotype, K).

Distribution. Pacific side of central Mexico (México to Guerrero) at elevations of ca. 1750 m (Fig. 8).

Additional specimens examined. MEXICO. **México:** *Hinton 1968* (K*), *Hinton 5004* (K), *Hinton 5211* (K), *Hinton 8257* (K). **Guerrero:** *Hinton 10978* (K*), *Hinton 11621* (K).

5. Echinopeon torquatus (DC.) Rose, Contr. U.S. Natl. Herb. 5: 118. 1897. *Elaterium torquatum* DC., Prodr. 3: 310. 1828. *Echinocystis torquata* (DC.) Cogn., Diagn. Cucurb. Nouv. 2: 88. 1877. TYPE: tab. 38, fig. C in Moç. & Sessé, Icones Fl. Mexic. ined. (holotype, G[4] n.v.).

[4] A reproduction of the plates in *Icones Fl. Mexic. ined.* can be found in A. DC., Calques Fl. Mexique. 1874 (BM!).

Figure 6. Photograph of the holotype of *Echinopepon tultitlanapaensis* (*Purpus 3548*, BM).—a. Habit.—b. Staminate flower. All scale bars in mm.

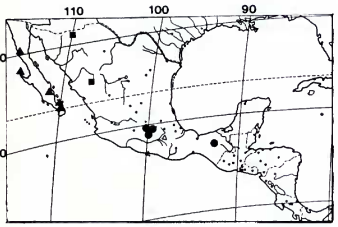

Figure 7. Distribution of *Echinopepon milleflorus* (●), *E. minimus* (▲), *E. wrightii* (■), and *E. tultitlanapaensis* (△).

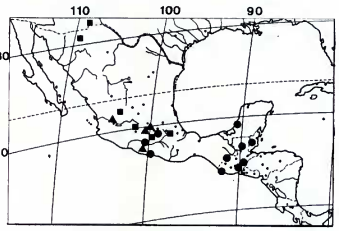

Figure 8. Distribution of *Echinopepon paniculatus* (●), *E. coulteri* (■), and *E. jaliscanus* (▲).

Echinopepon quinquelobatus Naudin, Ann. Sci. Nat., Bot. sér. 5, 6: 18. 1866. TYPE: *Bourgeau s.n.* (material cultivated in Paris from seed sent from Mexico by Bourgeau in 1865–1866) (holotype, P).

Distribution. The Pacific side of Mexico at elevations of 2000–2600 m (Fig. 9).

Additional specimens examined. MEXICO. Locality unknown: *Sessé et al. 4656* (MA n.v., photograph K). *Hahn 290* (P). **Baja California Sur:** *Barclay 3107* (BM). **Chiapas:** *Ortiz 1207* (F), *Breedlove 6769* (F*), *Breedlove 12431* (F*). **Distrito Federal:** *Bourgeau 1060* (K, P). **México:** *Hinton 7648* (K).

6. Echinopepon milleflorus Naudin, Ann. Sci. Nat., Bot. sér. 5, 6: 18. 1866. *Echinocystis milleflora* (Naudin) Cogn., Diagn. Cucurb. Nouv. 2: 88. 1877. TYPE: Mexico. *Bourgeau s.n.* (material cultivated in Paris from seed sent from Mexico by Bourgeau in 1865–1866) (holotype, P).

Distribution. Pacific side of central and southern Mexico at elevations of 1500–2640 m (Fig. 7).

Additional specimens examined. MEXICO. **Chiapas:** *Laughlin 963* (K), *Laughlin 1169* (K). **Distrito Federal:** *Pringle 6516* (BM*, K, P), *Pringle 6457* (BM*, K, P), *Roe 1516* (K), *Roe 1632* (K), *Rose & Painter 7121* (BM). **México:** *Hinton 8561* (K), *Hinton 7366* (K).

7. Echinopepon gemellus (DC.) A. K. Monro & Staff., comb. nov. Basionym: *Elaterium gemellum* DC., Prodr. 3: 310. 1828. *Echinocystis gemella* (DC.) Cogn., Diagn. Cucurb. Nouv. 2: 88. 1877. TYPE: tab. 38, fig. B in Moç. & Sessé, *Icones Fl. Mexic. ined.* (holotype, G n.v.).

Sicyos eremocarpus Peyr., Linnaea 30: 56. 1859–1860. TYPE: Mexico. *Heller 393* (lectotype, here designated, P); *Aschenborn s.n.* (syntype, not traced).

Distribution. Pacific side of central Mexico at elevations of ca. 2700 m (Fig. 9).

Additional specimens examined. MEXICO. **Distrito Federal:** *Schmitz 87* (BM). **Morelos:** *Schmitz 997* (BM), *Berlandier 1115** (BM).

This species was placed in the *Echinocystis* sect. *Echinopepon* by Cogniaux (1881). Rose did not incorporate this into the genus *Echinopepon* when this was resurrected by him (Rose, 1897) since he was unable to obtain herbarium material of this taxon.

8. Echinopepon coulteri (A. Gray) Rose, Contr. U.S. Natl. Herb. 5: 116. 1897. *Elaterium coulteri* A. Gray, Pl. wright. 2: 61. 1853. TYPE: Mexico. Zacatecas: *Coulter 51* (holotype, GH; isotype, K).

Echinopepon confusus Rose, Contr. U.S. Natl. Herb. 5: 115. 1897. TYPE: U.S.A. New Mexico: *Thurber 1122* (holotype, GH).

Echinopepon nelsoni Rose, Contr. U.S. Natl. Herb. 5: 117. 1897. TYPE: Mexico. Oaxaca: *Nelson 1878* (holotype, US).

Echinopepon parvifolius Rose, Contr. U.S. Natl. Herb. 5: 118. 1897. TYPE: Mexico. Oaxaca: *Conzatti 139* (holotype, US).

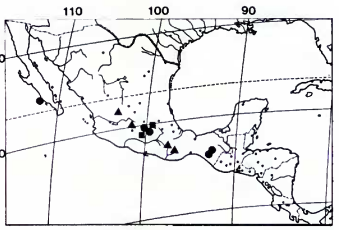

Figure 9. Distribution of *Echinopepon torquatus* (●), *E. pubescens* (▲), and *E. gemellus* (■).

Distribution. Southwestern United States (New Mexico) to southern Mexico (Veracruz) at elevations of ca. 2000–2350 m (Fig. 8).

Additional specimens examined. U.S.A. **New Mexico:** *Metcalfe 1348* (BM*), MEXICO. **Distrito Federal:** *Bourgeau 789* (K, P), *Hahn 162* (P*). **Guanajuato:** *Haag & Schmidt 598* (K). **Morelos:** *Bourgeau 1388* (P), *Greene 17011* (K). **Veracruz:** *Nee & Soulé 33055* (K*). **Zacatecas:** *Wright s.n.* (K), *Rose 2699* (K).

Balls & Gourlay 530 (BM), collected in Puebla, Mexico, at 2600 m elevation, differs from all other specimens examined in having significantly larger flowers and relatively longer stamens.

9. Echinopepon cirrhopedunculatus Rose, Contr. U.S. Natl. Herb. 5: 115. 1897. TYPE: Mexico. Sonora: *Palmer 634* (holotype, US; isotype, K).

Distribution. Northern to central Mexico at elevations of ca. 500–1000 m (Fig. 5).

Specimens examined. MEXICO. **Chihuahua:** *Gentry 2355* (K). **Guerrero:** *Hinton et al. 10496* (K, P). **Jalisco:** *Pringle 4562* (BM*). **México:** *Hinton 1364* (K*), *Hinton 9257* (K), *Hinton 6438* (K), *Hinton 8483* (K).

10. Echinopepon arachoides (Dieterle) A. K. Monro & Staff., comb. nov. Basionym: *Apatzingania arachoidea* Dieterle, Brittonia 26: 131. 1974. TYPE: Mexico. Michoacán: *Dieterle 4379* (holotype, MICH n.v.; isotype, K).

Distribution. Pacific Coast of Mexico (Michoacán to Guerrero) at an elevation of ca. 300 m.

Additional specimen examined. MEXICO. **Guerrero:** *Hinton 6424* (K*).

11. Echinopepon minimus (Kellogg) S. Watson, Proc. Amer. Acad. Arts 24: 52. 1889. *Marah minima* Kellogg, Proc. Calif. Acad. Sci. 2: 18. 1863. *Elaterium minimum* (Kellogg) S. Watson, Proc. Amer. Acad. Arts 12: 252. 1877. TYPE: Mexico. Baja California Sur: Cedros Island, *Streets s.n.* (lectotype, designated by Stocking (1955), US n.v.; isolectotypes, GH n.v., NO photograph).

Distribution. Limited to Baja California Sur at elevations of ca. 200–1000 m (Fig. 7).

Additional specimens examined. MEXICO. **Baja California Sur:** *Brandegee s.n.* (K photo, US), *Palmer 719* (K), *Anthony 299* (K), *Gentry 4125* (K), *Palmer 65* (K), *Wiggins 14436* (K*), Aug. 1859–Jan. 1860, *Xantus de Vesey* (GH).

12. Echinopepon paniculatus (Cogn.) Dieterle, Fieldiana, Bot. 24(11): 342. 1976. *Echinocystis paniculata* Cogn., Diagn. Cucurb. Nouv. 2: 90. 1877. TYPE: Mexico. Guerrero: *Galeotti s.n.* (holotype, BR).

Distribution. Central Mexico (Guerrero) to southern Guatemala (Chiquimula) at elevations of 50–1360 m (Fig. 8).

Additional specimens examined. MEXICO. **Campeche:** *Andres & Nee 157* (K). **Chiapas:** *Lira et al. 930* (BM), *Lira et al. 942* (BM), *Soto 13269* (BM). **Guerrero:** *Mexía 8703* (K), *Hinton 6623* (K), *Hinton 8509* (K). BELIZE. *Bartlett 12882* (F), *Lundell 2190* (F), *Liesner & Dwyer 1626* (K, MO). GUATEMALA. Locality unknown: *Bernoulli & Cario 2838* (K). **Chiquimula:** *Standley 73737* (F). **Huehuetenango:** *Molina 21325* (F), *Molina & Molina 30171* (F, MO), *Williams 41113* (F*), *Williams 41364* (F*). **Jalapa:** *Standley 77384* (F), *Standley 76495* (F*). **Petén:** *Ortiz 547* (MO*).

13. Echinopepon glutinosus (Cogn.) A. K. Monro & Staff., comb. nov. Basionym: *Echinocystis glutinosa* Cogn., Diagn. Cucurb. Nouv. 2: 93. 1877. TYPE: *Bourgeau s.n.* 1866 (material cultivated in Paris in 1867 from seed sent from Mexico by Bourgeau in 1866) (holotype, P*).

Distribution unknown. Mexico; known only from the type collection.

This species was placed in *Echinocystis* sect. *Echinopepon* by Cogniaux (1881). Rose did not incorporate this into the genus *Echinopepon* when this was resurrected by him (Rose, 1897), since he had been unable to obtain herbarium material of this taxon.

14. Echinopepon wrightii (A. Gray) S. Watson, Bull. Torrey Bot. Club 14: 158. 1887. *Elaterium wrightii* A. Gray, Pl. wright. 2: 61. 1853. TYPE: Mexico. Sin. loc., *Wright 1090* (holotype, US; isotypes, GH-257*, -259* & -260).

Distribution. Central Mexico at elevations of ca. 1000–2000 m (Fig. 7).

Additional specimen examined. MEXICO. **Zacatecas:** *Emory 397* (K).

The GH isotype contains two different types of pollen: sheet 260 has zonocolpate, spinulose pollen of a type found in the Sicyinae, whereas sheets 257 and 259 have 7–9-zonocolpate, non-spinulose pollen similar to that of the holotype. It is not, however, possible to say with any certainty whether this is the result of a mixed collection or whether this species has dimorphic pollen, since sheet 260 does not have any additional, sufficiently mature flowers from which to draw a conclusion.

15. Echinopepon pubescens (Benth.) Rose, Contr. U.S. Natl. Herb. 5: 118. 1897. *Elaterium pubescens* Benth., Pl. hartw. 6. 1839. *Echinocystis pubescens* (Benth.) Cogn., Diagn. Cucurb. Nouv. 2: 88. 1877. TYPE: Mexico. Aguascalientes: *Hartweg 15* (holotype, K; isotype, BM*).

Echinocystis floribunda Cogn., Diagn. Cucurb. Nouv. 2: 89. 1877. *Echinopepon floribundus* (Cogn.) Rose, Contr. U.S. Natl. Herb. 1: 116. 1897. TYPE: Mexico. Oaxaca: *Liebmann 53* (syntype, B missing and probably destroyed); *Liebmann 28* (syntype, B missing and probably destroyed); *Galeotti 1890* (lectotype, here designated, P; isolectotypes, G, K, W).

Distribution. Central to southern Mexico (Aguascalientes to Oaxaca) at elevations of ca. 1500–1800 m (Fig. 9).

Additional specimens examined. MEXICO. Locality unknown: *Hartweg s.n.* (K). **Michoacán:** *Pringle 4346* (BM*, K). **Oaxaca:** *Galeotti 1890* (K, P), *Pringle 4957* (BM*, K), *Purpus 4204* (BM*, K), *Rose 11313* (K).

16. Echinopepon longispinus (Cogn.) Rose, Contr. U.S. Natl. Herb. 5: 117. 1897. *Echinocystis longispina* Cogn., Diagn. Cucurb. Nouv. 2: 91. 1877. TYPE: Mexico. Veracruz: *Schiede 1080* (lectotype, here designated, GH; isolectotype, B missing and probably destroyed).

Distribution. Central Pacific side of Mexico at elevations of ca. 1200 m.

Additional specimens examined. MEXICO. **Morelos:** *Pringle 11301* (K), *Ravias 541* (P), *Hahn s.n.* (K, P).

17. Echinopepon belizensis A. K. Monro & Staff., sp. nov. TYPE: Belize. Cayo: El Cayo, *Bartlett 11989* (holotype, NY*; isotypes, GH, US). Figure 10a, b.

E. pubescenti (Benth.) Rose affinis, sed hypanthio latissimo brevissimoque, corollae lobis brevibus latisque, corollae glandis pedicellatis, antheris subsessilibus, bene differt.

Leaves ca. 5.0–7.5 × 4.5–7.0 cm, lobate, membranous, upper surface puberulous and minutely pustulate, lower surface puberulous, lobes 3, 5, or 7, the base cordate, the margins remotely denticulate, the apex acuminate; petiole ca. 30–50 × 1 mm, densely puberulous; tendrils bifid, ca. 4.5 cm long before branching. Staminate flowers ca. 12–20, borne in a panicle ca. 60 mm long, bearing flowers for ⅔ of its length; pedicels ca. 11 × 0.2 mm, puberulous; hypanthium ca. 1 × 2 mm, patelliform, glabrous; calyx lobes dentate, ca. 0.5 mm long, glabrous; corolla ca. 5–6 × 10–12 mm, patelliform, fused for ⅓ of its length, inner surface stalked glandular, outer surface farinaceous, lobes ovate, the apices acuminate; filaments ca. 0.1 mm in length, fused; anthers ca. 1–1.5 mm in length, fused to form an ovoid to obovoid head 0.5–0.8 mm diam., subsessile; unilocular and bilocular thecae semi-sigmoid or "J"-shaped, microechinate; pollen ca. 7-zonocolporate, radially asymmetrical (there may be a raised annulus-like structure encircling the pore, as present in the related genus *Rytidostylis*, clearly seen in SEM but indistinct in LM). Pistillate flowers 1-2, solitary or borne in a fascicle; pedicel ca. 4–15 × 0.5 mm, glabrous, sparsely puberulous; hypanthium ca. 2.5 × 4 mm, campanulate, sparsely puberulous, constricted at base, constriction ca. 3.5–4.5 × 0.5 mm, densely puberulous; calyx lobes ca. 0.5 mm long; corolla ca. 7 × 9 mm, narrowly patelliform, fused for ⅓ of its length, inner surface stalked glandular, outer surface glabrous, lobes ovate, the apices acuminate; ovary ca. 3–4 mm, ovoid, puberulous, spines ca. 1.5–3 mm; style ca. 0.5 mm, glabrous; stigma ca. 0.8 × 1 mm. Fruit not seen.

Distribution. Known only from the type collection made at 200 m (Fig. 5).

This species most closely resembles *Echinopepon pubescens* in having ovoid anthers and zonocolporate pollen. It differs, however, in hypanthium shape, corolla shape, corolla indument, and anther disposition. The staminate and pistillate perianths in *E. pubescens* are composed of a relatively long, narrow campanulate hypanthium from which spread out the deeply divided, long, narrow and recurving corolla lobes; in *E. belizensis*, however, the hypanthium is very broad, and plate-like, the corolla lobes less divided, shorter, broader and not recurved. The glands covering the inner surface of the corolla lobes are stalked in *E. belizensis* and sessile to subsessile in *E. pubescens*. The anthers of *E. belizensis* are subsessile, while those of *E. pubescens* are supported by a filament 1–1.5 mm long. The two species also differ greatly in their altitudinal ranges, *E. pubescens* not having been collected below 1500 m while *E. belizensis* was collected at ca. 200 m.

18. Echinopeon micropaniculatus A. K. Monro & Staff., sp. nov. TYPE: Costa Rica. Guanacaste: 2 km E of Hacienda Palo Verde, Comelco property, *Keeler 192* (holotype, MO*). Figure 11a, b.

E. paniculato (Cogn.) Dieterle affinis, sed floribus minoribus, antheris ovoideis, bene differt.

Leaves ca. 6–10 × 5–9.5 cm, lobate, subchar-

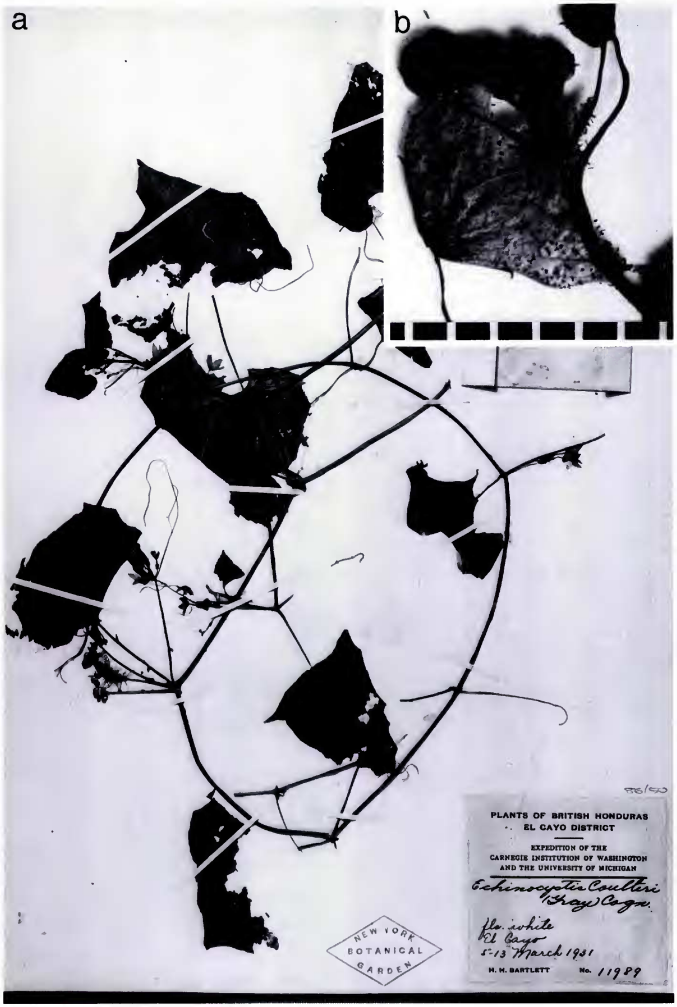

Figure 10. Photograph of the holotype specimen of *Echinopepon belizensis* (*Bartlett 11989*, NY).—a. Habit.—b. Staminate flower. All scale bars in mm.

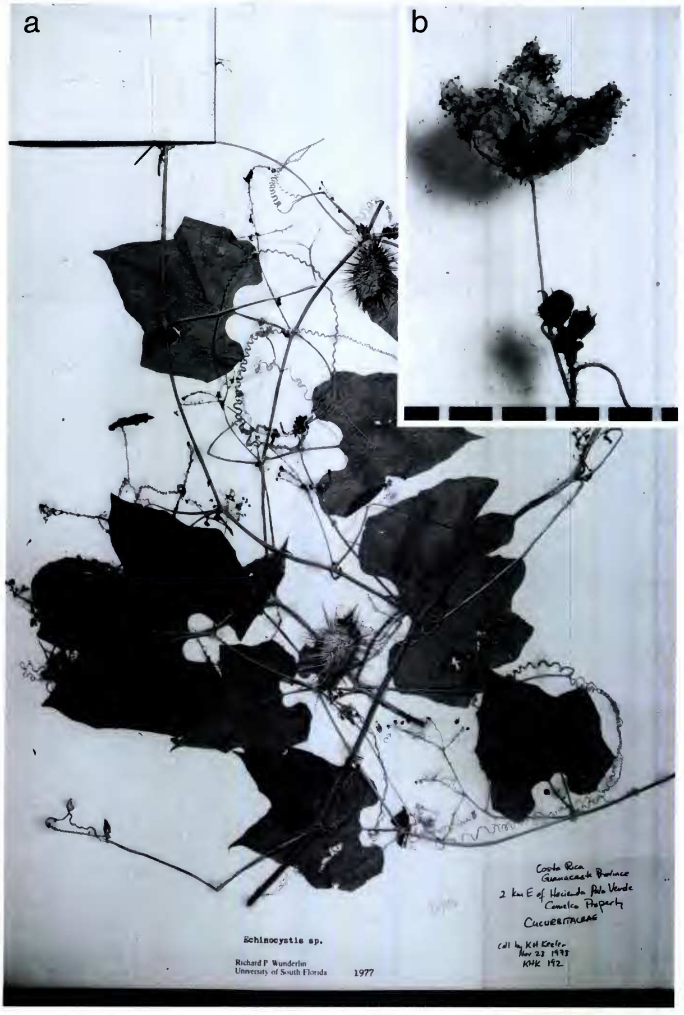

Figure 11. Photograph of the holotype specimen of *Echinopepon micropaniculatus* (*Keeler 192*, MO).—a. Habit.—b. Staminate flower. All scale bars in mm.

taceous to chartaceous, upper and lower surface villous, lobes 3, 5, or 7, the base sagittate to cordate, the margins remotely denticulate, the apex acuminate; petiole ca. 25–40 × 1.5–2 mm, densely villous; tendrils trifid, ca. 2.5–9.0 cm long before branching. Staminate flowers ca. 50–60, borne in a panicle ca. 80–100 mm long bearing flowers for ⅓–½ of its length; pedicels ca. 3–5 × 0.3 mm, pilose; hypanthium ca. 1.5 × 2 mm, broad campanulate to patelliform, glabrous; calyx lobes deltate, ca. 0.3 mm long; corolla ca. 2 × 3 mm, patelliform to broadly campanulate, fused for ½ of its length, inner surface subsessile, outer surface glabrous, lobes elliptic to ovate, the apices acute to obtuse; filaments ca. 1.5 mm in length, fused; anthers ca. 1 mm in length, fused to form an ovoid to obovoid head 0.4 mm diam.; unilocular and bilocular thecae semi-sigmoid or "J"-shaped, glabrous; pollen ca. 6-zonocolporate, radially asymmetrical. Pistillate flowers not seen. Fruiting peduncle ca. 5 mm, pilose; fruit ca. 30 × 14 mm; spines ca. 15–16 mm, sparsely pilose; seeds 2 per locule, ca. 6 × 3.5 × 1–1.5 mm, rectangular, armored.

Distribution. This species is known only from the type collection (Fig. 5).

Echinopeon micropaniculatus most closely resembles *E. paniculatus* in the morphology of the perianth and pollen. It differs significantly, however, in flower size and anther structure. The flowers of *E. micropaniculatus* are ca. 3 mm in diameter, while those of *E. paniculatus* are 7–14 mm in diameter.

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